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THE ENERGY ENVIRONMENT OF THE ALPINE TUNDRA *

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ABSTRACT

The climate of the alpine tundra is described in terms of the energy exchange involving radiation, convection, and transpiration. The radiation budget of the alpine environment is described in detail with particular emphasis on the ultraviolet. The wind profile of a fell field in the tundra is described. Leaf temperature measurements of alpine plants are reported. An evaluation of the energy exchange and the leaf temperature of *Polygonum bistortoides* is given.

RESUME

L'auteur décrit le climat de la toundra alpine en fonction de l'échange d'énergie qui comprend radiation, convection et transpiration. Le bilan des radiations du milieu alpin est décrit en détail en mettant l'accent sur les stations montagneuses de la toundra. Il donne également des résultats de mesures de températures foliaires.

Il procède enfin à une évaluation de l'échange d'énergie et de la température foliaire de *Polygonum bistortoides*.

ZUSAMMENFASSUNG

Das Klima des alpinen Tundra wird in Hinsicht des Energieaustausches beschrieben. Dieser umfasst die Austrahlung, die Konvektion und die Transpiration. Der Bestrahlungshaushalt in der alpinen Stufe wird eingehend behandelt mit besonderer Berücksichtigung der Ultraviolettbestrahlung. Der Verfasser beschreibt auch das Windprofil eines bergigen kahlen Standortes der Tundra. Er gibt ebenso die Ergebnisse von Blatttemperatur-Messungen. Energieaustausch und Blatttemperatur von *Polygonum bistortoides* wurden gemessen.

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INTRODUCTION

Climate has its influence on organisms, bodies of water, or other objects in terms of the flow of energy. Energy means life and warmth, motion and activity, process and change. The alpine zone is never static, constantly in a state of change: physical, chemical, and biological progressions by which energy is transferred, modified, and consumed. Nowhere are these activities more vigorously displayed than in the alpine environment.

Energy can be transferred in the form of radiation, convective flow by the movement of the air, and by the exchange of moisture. Energy is consumed with the evaporation or transpiration of moisture and is released with condensation. The alpine tundra is characterized by wind, which is frequent and variable, more turbulent than laminar, and more often cold than warm; calm days are rare in the open, but more frequent in sheltered microsites. The wind conditions are dramatically different at 10 meters height, 1 meter, and 1 centimeter. Trees which would otherwise project straight up and grow well are stunted, twisted, and sheared to grow nearly horizontal to form krumholtz. All life hugs the ground, plants grow low, insects remain near the surface, and mammals move within the soil and on the surface out of the wind.

Moisture in the alpine tundra is highly variable in amount and form. It may fall as rain, sleet, hail, or snow; blow away, run off, evaporate or sublime; percolate into the soil, fill small depressions, form snowbanks, glaze the surface with ice, expand on freezing to break rocks, force up soil, or in various ways to exert change upon the microtopography of the alpine environment. During summer and autumn a micro « desert » may exist a few feet from a sodden micro « marsh ». An abundance of water, if it is in frozen form, may result in an abundance of available water for life. Many microsites of the alpine tundra are literally frozen deserts.

The cosmic cold of space drains the radiant energy from the alpine tundra through brilliantly clear skies at night and the dawn breaks with the suddenness and intensity of an avalanche as the sun's rays from the east penetrate the transparent sky. The discontinuity of the dawn is dramatic; figures and forms on the surface suddenly receive the stimulus of light and heat; everything is clearly alive and vital. In phase and out of phase, leading and lagging, life renews as the sunlight penetrates every nook and cranny, soaks in, warms the granitic masses and heats the soil. For the roots of plants and the burrow habitats of animals, the dramatic dawn is mellowed and dulled, the change is slow, and the awakening is gradual. For plants, the aerial part have received the sharp stimulus of the striking sun when the buried regimes are frozen and slowed. A mammal or insect below the surface may realize hours later the excitement of the day and emerge to share in the

activity above or remain submerged in the dampened darkness as the warmth of the surface penetrates below.

By midday in summer the brilliance of the sunlight is supreme, the actinic ultraviolet of the solar spectrum on the mid-latitude alpine tundra is severe, and the total caloric flux from the sun may be greater than, or as great as, the solar flux at any other locale on earth. If during periods with clear, transparent skies, broken cumulus clouds scatter overhead, the total solar radiation received by a horizontal surface may exceed the solar constant. The amount of sunlight reaching the earth, on a surface perpendicular to the solar rays outside the atmosphere, is known as the solar constant and is approximately $2.0 \text{ cal. cm}^{-2} \text{ min}^{-1}$.

It is these factors, radiation, convection, evaporation, and temperature with which this paper is concerned in dealing with the energy exchange of the alpine tundra.

SOLAR RADIATION

The high intensity of the solar radiation incident on the alpine tundra of mid-latitudes during the summer is the consequence of clear air of low density. The atmosphere above the Rocky Mountains is generally more turbulent and dusty than the air above the coastal Sierra Nevada Mountains where late summer days exhibit a remarkable clarity. The increased transparency of the sky with altitude results from a reduction in dust, which reduces the amount of scattering, a reduction in the amount of water vapor overhead, which strongly reduces the amount of absorption at infrared wavelengths, and a reduction in molecular scattering at ultraviolet and visible wavelengths. A slight reduction of attenuation due to the falling off of other constituents occurs. However, due to the fact that some of these, such as ozone, are concentrated in the stratosphere, the change with altitude at the surface of the earth has little influence.

The spectral distribution of the extraterrestrial solar radiation incident upon a surface normal to the sun's rays is shown as the uppermost curve of fig. 1. This is plotted on a wavenumber scale in cm^{-1} which is the reciprocal of the wavelength and is directly proportional to the frequency of the light. A plot of this type has the advantage that the full spectrum of interest readily can be shown on a single scale, whereas a wavelength plot has difficulty including the visible and infrared together. The total area under the upper curve of fig. 1 is $2.0 \text{ cal cm}^{-2} \text{ min}^{-1}$, the solar constant.

The sunlight passing through the earth's atmosphere is attenuated by oxygen and ozone absorption and by molecular scattering on the short wavelength, high frequency, ultraviolet end of the spectrum and by water vapor and carbon dioxide

absorption in the long wavelength, low frequency, infrared end. In addition, there is scattering throughout the spectrum caused by dust and haze particles present in the atmosphere. Since the amount of dust present in the atmosphere is highly variable and during extremely clear days at high elevations is essentially absent, the attenuation by dust will be omitted from the following discussion which will pertain only to clear skies.

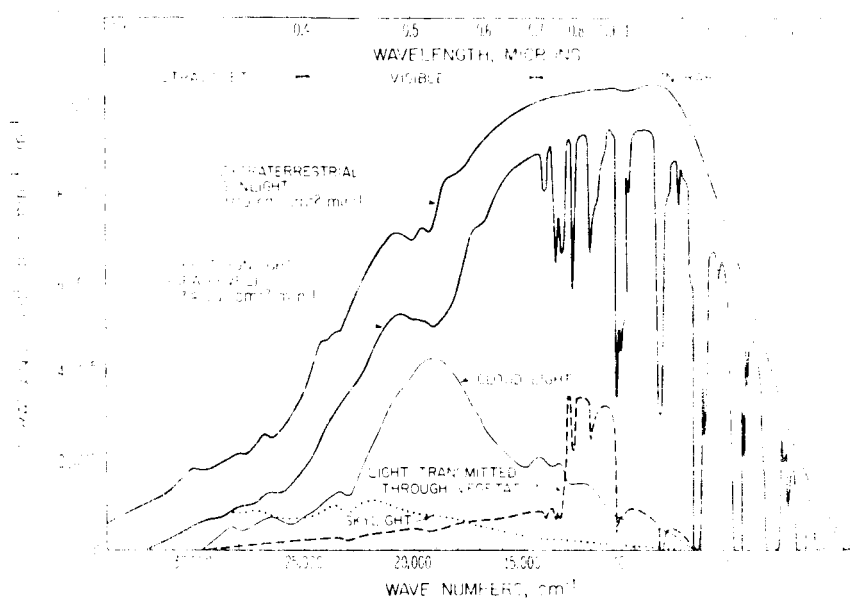


Fig. 1. Spectral distribution of direct solar radiation from the zenith outside the earth's atmosphere, at the surface at 15,000 ft. above sea level. Also shown are the spectral distribution for cloud light and sky light.

The transmission, T , of the atmosphere to radiation of a particular wavelength, λ , can be represented by the following relationship:

$$\frac{\lambda I}{\lambda I_0} = e^{-k(\lambda) u \sec z} \quad (1)$$

where I_0 is the intensity of the incident monochromatic radiation of wavelength, λ , entering the atmosphere, I is the intensity after passage through an amount of absorbing constituent, u , z is the solar zenith angle, and $k(\lambda)$ is the extinction coefficient which depends upon the absorbing or scattering substance and the wavelength. The extinction coefficient is a rapidly varying function of the wavelength.

In order to determine the spectral distribution of the solar radiation reaching the earth's surface, it is necessary to know the extinction coefficient for each wavelength. The ultraviolet terminus of the solar energy reaching the earth's surface is primarily due to ozone. Absorption coefficients for ozone are listed

in the Handbook of Geophysics (1961). Since the amount of ozone in the atmosphere is primarily in the stratosphere, only a change in the ozone amount far above the surface can produce any significant increase or decrease in the ultra-violet content of the sunlight reaching the surface. The greatest change in total ozone amount is seasonal, rather than diurnal, and can be characterized by values between 0.2 and 0.3 atmos-cm of ozone, see Goody (1954). For these amounts of ozone the transmissivity of the atmosphere to solar radiation absorbed only by ozone is shown in Fig. 2. The very abrupt cut off due to ozone should be noted. The ozone is a vital screening layer which protects life on earth from the actinic rays of the sun.

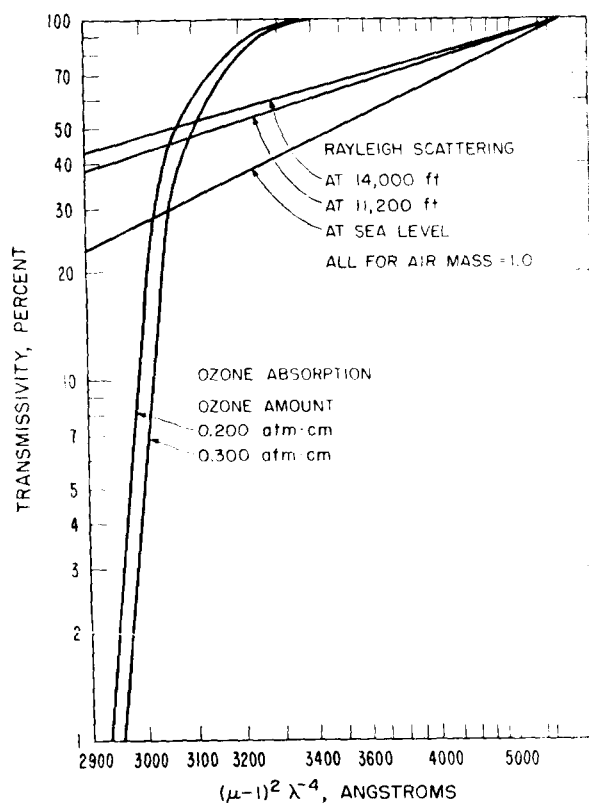


FIG. 2. — Spectral transmissivity of the zenith atmosphere due to ozone absorption and Rayleigh scattering by air molecules. The wavelength is non linear in order that the Rayleigh scattering function be a straight line.

On the other hand, molecular scattering, also referred to as Rayleigh scattering, is an effective attenuator of solar radiation and does change with altitude at the surface. The extinction coefficient due to molecular scattering has been described

by PENNDORF and his values are used for computing the transmissivity of the atmosphere by scattering alone as shown in Fig. 2. The most important feature of Rayleigh scattering is the inverse fourth power of the wavelength variation of the extinction coefficient ${}_s k(\lambda)$, with a small correction for the variation of the refractive index of the air with wavelength as follows:

$${}_s k(\lambda) \propto \frac{(\mu - 1)^2}{\lambda^4} \quad (2)$$

where λ is the wavelength and μ is the index of refraction.

This is the reason for using the abscissa scale as shown in Fig. 2, since the scattering component then is linear on such a plot. It is seen from Fig. 2 that the Rayleigh scattering component is particularly effective in reducing the intensity of solar radiation through the visible and near ultraviolet. It is also noted that the change in transmissivity with altitude, when comparing the sea level value with the value in the alpine tundra, is considerable for direct solar radiation transmitted through the zenith atmosphere. At a wavelength of 3100 Å the sea level transmissivity for radiation through the vertical would be about 30 %, while at 14000 feet it would be 50 %. For slant paths through the atmosphere the effect is much more striking.

The total attenuation of direct ultraviolet sunlight for clear skies in the alpine and at sea level is shown in Fig. 3 for an air mass, $\sec z = 1.05$, corresponding to a zenith angle, $z = 18^\circ$, and for $\sec z = 2.00$, or a zenith angle, $z = 60^\circ$. At noon on the summer solstice the sun will reach a zenith angle of 18° at a latitude of 40.5° . The attenuation shown here is solely due to ozone absorption and Rayleigh scattering and does not include attenuation caused by dust in the atmosphere. The values given in Fig. 3 represent the maximum transparency the sky should attain with only a slight improvement during periods of low ozone concentration. The curves represent ozone amounts of 0.250 atmosphere centimeters, an approximate mean value.

Because of the great importance of ultraviolet radiation to alpine plants and animals, it is useful to evaluate this portion of the spectrum with particular care. Figure 4 shows an expanded plot of the distribution of the extraterrestrial solar energy as a function of the wavelength. This plot is based on data from DUNKELMAN and SCOLNIK (1954). The energy has been averaged over 100 Å intervals in order to smooth out the stronger variations which occur with wavelength. The solar irradiance is strongly variable in the ultraviolet, although this variability does not show up in the total energy, i.e. in the value of the solar constant.

Among the biological effects of ultraviolet radiation on organisms is its influence on human skin in the form of sunburn or tanning of the skin. The relative action spectrum curve for erythema, or reddening of the skin, is shown in Fig. 4 as taken from BLUM (1959). The strong peak at 2950 Å should be noted

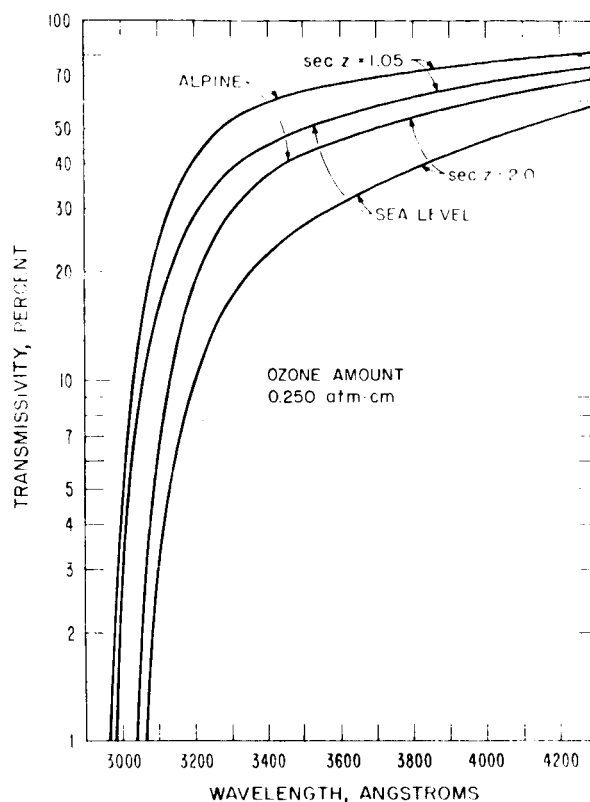


FIG. 3. — Spectral transmissivity of the atmosphere for the alpine undra at 12 to 14,000 feet above sea level and the sea level values for air mass 1.05 (zenith angle 18°) and air mass 2.0 (zenith angle 60°)

and the fact that wavelengths longer than 3200 Å are not effective. Toward shorter wavelengths there is a minimum at 2800 Å and then at shorter wavelengths yet the erythral activity rapidly increases again (not shown in Fig. 4). After a suntan has begun to bleach, its color may be restored to some extent by exposure to wavelengths from 3000 Å to 4000 Å. The action spectrum for pigment darkening is also shown in Fig. 4. It is clear that man exposed to the full extraterrestrial ultraviolet sunlight would be seriously if not fatally burned and that various carcinogenetic effects would also occur, see BLUM (1959). Wavelengths shorter than 3200 Å cause skin cancer in man. As will be seen later, the amount of sunlight received at the earth's surface near sea level of wavelengths shorter than 3200 Å is very small. However, skin cancers do occur in men at sea level whose occupations keep them out of doors. At higher elevations the amount of radiation shorter than 3200 Å is substantially increased, see Fig. 5. According to Lave-

RENS and MAYERSON (1932) the main antirachitic component of solar radiation consists of wavelengths shorter than 3130 Å.

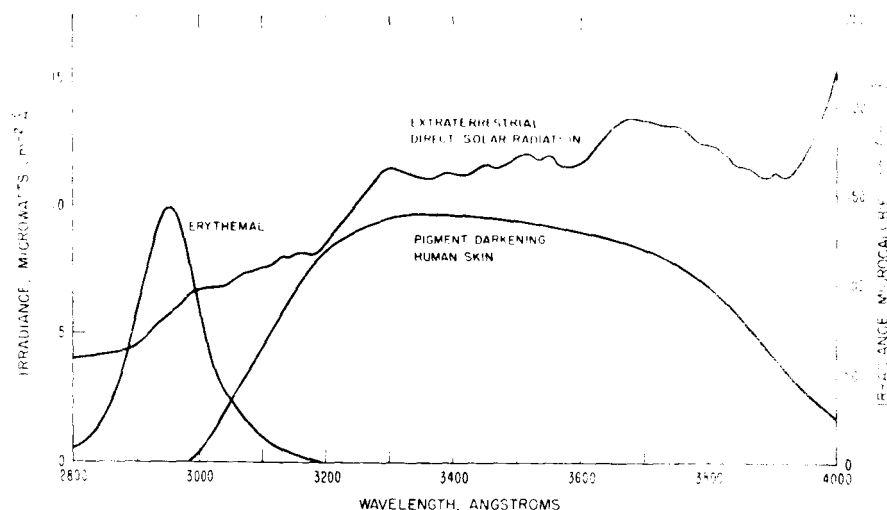


FIG. 4. — Intensity of the extraterrestrial ultraviolet solar radiation as a function of wavelength and the relative action spectra for erythema and pigment darkening of human skin.

It is the amount of ultraviolet sunlight at the earth's surface with which we are to be concerned here. From the transmissivity curves of Fig. 3, and the extraterrestrial solar radiation shown in Fig. 4, it is possible to compute the amount of direct ultraviolet sunlight received at the surface. However, in addition to direct sunlight there is a strong amount of scattered skylight which in the ultraviolet often is greater than the direct sunlight. There is very little observational data concerned with the scattered ultraviolet skylight. The best source of information is a report by BENER (1960) concerning observations he made at Davos, Switzerland. However, BENER's data is for an altitude of 1950 meters above sea level and some allowance must be made for using it as an indication of what may be the situation at higher altitudes. An analysis of BENER's data was made so that ratio of skylight to direct sunlight for various wavelengths was determined as a function of the air mass. The situation would appear to be that the ratio of skylight to direct sunlight is approximately 1.0 at an air mass of 1.2 and 2.0 for an air mass of 2.0. It was considered from this that in the alpine the ultraviolet skylight would just about equal the direct ultraviolet sunlight for an air mass of 1.05 and would be double the amount of ultraviolet sunlight for an air mass of 2.0. On this basis the curves representing the total amount of incident solar ultraviolet radiation (direct sun plus diffuse skylight) received on an exposed horizontal surface would be as shown in Fig. 5. The curves for the

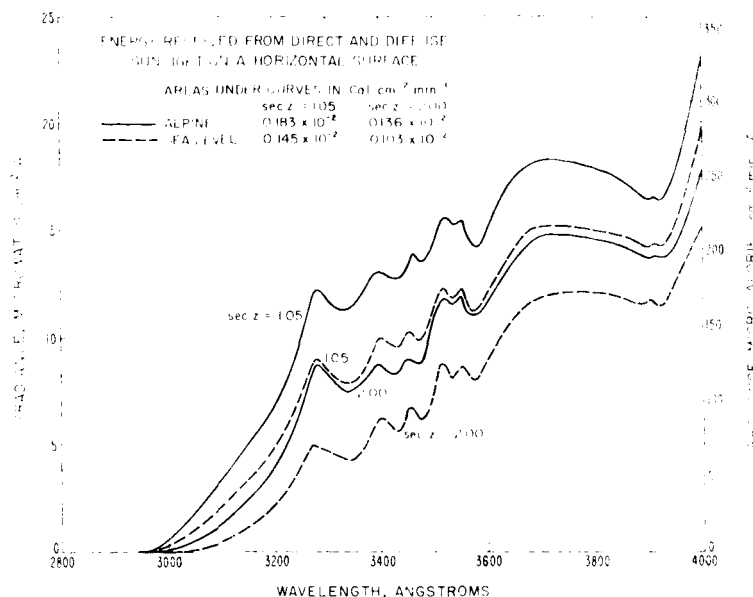


FIG. 5. — Spectral distribution of total sunlight (direct and diffuse) incident on a horizontal surface in the alpine at 12000 feet above sea level and at sea level for zenith angles of 18° (sec z = 1.05) and 60° (sec z = 2.00) for a clear day.

alpine may be somewhat underestimated and those for sea level overestimated, however, in general it should represent a reasonable comparison for the various clear sky conditions. The areas under the curves are given in Fig. 5 and it is evident that the alpine receives substantially more ultraviolet energy than does the surface at sea level. The total energy shorter than 3200 Å is 1.00×10^{-2} cal cm⁻² min⁻¹ for the alpine with air mass 1.05, and 0.44×10^{-2} at air mass 2.0, while for sea level the amounts are 0.67×10^{-2} for air mass 1.05 and 2.0 respectively. Hence, at air mass 1.05 the alpine is irradiated with 1.5 times as much short ultraviolet (< 3200 Å) and with 2.2 times as much at air mass 2.0. It is somewhat surprising that in going from sea level to altitudes of about 12000 feet the increase in ultraviolet radiation is not more substantial. The greater presence of dust at lower elevations will play an enormous role toward reducing the sea level values for many cloudless days. According to LAURENS and MAYERSON (1932) there is, nevertheless, ample antirachitic component of sunlight (< 3130 Å) at New Orleans during midsummer and they give measured values of 10^{-1} cal cm⁻² min⁻¹.

Observations of the ultraviolet radiation of wavelengths shorter than 4100 Å incident at various altitudes in the Rocky Mountains have been made by MERICLE and MERICLE (1964). Their results of clear days are shown in Fig. 6 which gives

the total integrated energy from 2900-4100 Å for direct sunlight, as a function of the time day, at elevations of 11,400, 9600, 8600, and 7800 feet. The values do not include the skylight and are approximately one-half the magnitude of the values obtained by integrating the areas under the curves of Fig. 5. The curves are a good indication of the diurnal variation of the ultraviolet incident at the surface for a clear day. The ratio of the ultraviolet received for air mass 2.0 occurring at 7 : 15 a. m. to air mass 1.05 at noon gives nearly the same ratio for MERICLE's data and for the areas in Fig. 5.

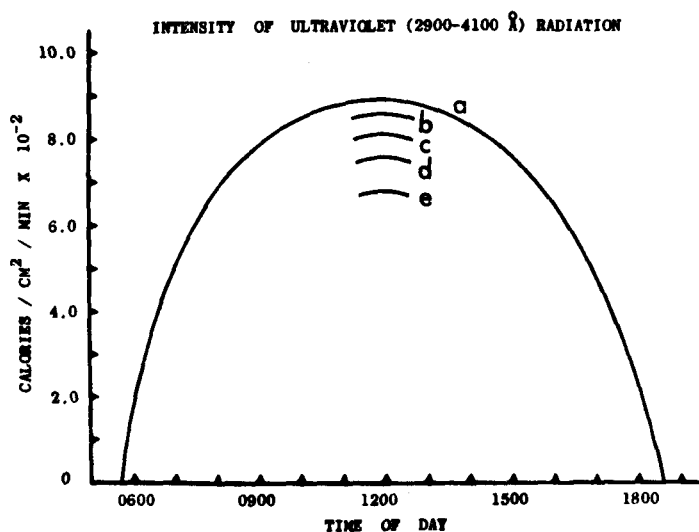


FIG. 6. — Diurnal variation of the observed intensity of ultraviolet in direct sunlight excluding skylight during clear days in the Colorado Rocky Mountains near latitude 40° N at the following locations: a) Summit of Mt. Evans, 14,200 ft. (4,330 m); b) Niwot Ridge, 11,400 ft. (3,473 m); c) Science Lodge, 9,600 ft. (2,930 m); d) Central City 8,600 ft. (2,625 m); and e) Raymond, 7,800 ft. (2,380 m). Data taken by L. W. Mericle and R. Mericle.

Throughout the visible portion of the spectrum the attenuation of solar radiation by the atmosphere is primarily caused by scattering. However, in the infrared portion of the spectrum, where nearly 50 % of the extraterrestrial energy from the sun is located, strong attenuation is caused by absorption due to atmospheric water vapor and carbon dioxide. These absorption bands are evident in Fig. 1. There is dramatically more infrared solar energy received in the alpine than at sea level and this is important for the existence of life at these elevations. The infrared solar radiation absorbed by plants plays an essential role in warming them and keeping their temperatures at a level sufficient for active photosynthesis

and other physiological processes. Unfortunately, plants have a characteristically strong reflectance in the near infrared, as shown in Fig. 7 and are not able to take as much advantage of this additional radiation as otherwise they might. This same high reflectance, however, is a protective mechanism to prevent them from burning up when the air temperature is high, particularly at lower elevations.

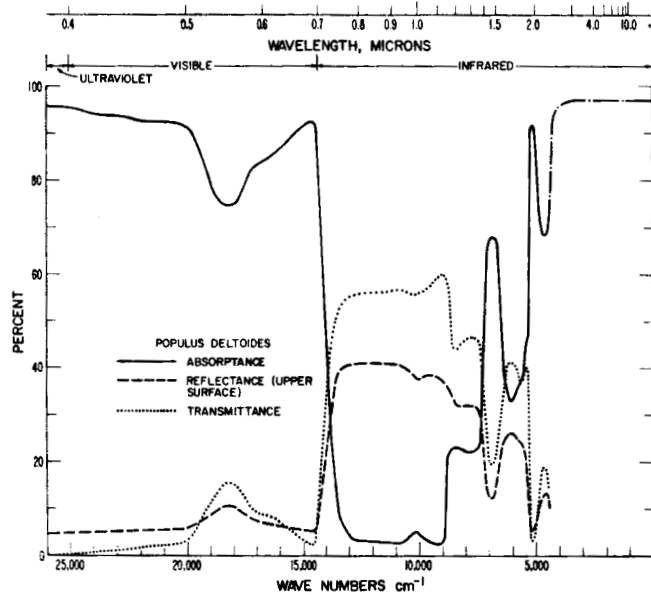


FIG. 7. — Spectral absorptance, reflectance, and transmittance of *Populus deltoides* leaf as a function of the frequency of the radiation in wavenumbers. A wavelength scale is given at the top. A wavenumber is the reciprocal of the wavelength and is proportional to the frequency.

ENERGY EXCHANGE

The plants on the surface, sandwiched between ground and sky, irradiated with sunlight, exchanging radiant energy, cooled and dried by wind, and cooled by transpiration are subjected to the following energy budget :

$$a_1 (S + s) + a_2 r (S + s) + a_3 (R_g + R_a) - 2 \epsilon_t \sigma T_l^4 \pm 2 C - 2 LE = 0$$

where a_1 is the absorptivity of the leaf to sunlight, a_2 is the absorptivity to reflected sunlight, r is the reflectivity of the ground to sunlight, S and s are the direct and diffuse sunlight respectively, a_3 is the absorptivity of the leaf to long wave thermal radiation, R_g and R_a are the long wave thermal radiation emitted by

ground and sky respectively, $\epsilon_t = a_3$ is the thermal emissivity of the leaf, σ is the Stefan-Boltzman constant for blackbody radiation, T_λ is the leaf temperature in $^\circ\text{K}$, C is energy exchange by convection, E is the transpiration rate in $\text{gm cm}^{-2} \text{min}^{-1}$ and L is the latent heat of vaporization. Two additional terms could be considered in the above equation. A term for energy consumed by the leaf in photosynthesis, which is small compared to the terms given, and a storage term for non-steady state situations.

Two types of convection may occur which will transfer energy to or from an organism; free convection in relatively still air, and forced convection in windy air. From heat transfer theory, and from specific experiments concerned with plants, GATES (1962), GATES and BENEDICT (1963), TIBBALS, CARR, GATES and KREITH (1964) and GATES, TIBBALS, and KREITH (1965) have shown that the energy exchange by convection can be determined experimentally. For a narrow flat leaf, such as that of *Polygonum*, the following formulae give a reasonable approximation for convection. For free convection:

$$C_f = 6.0 \times 10^{-3} \left(\frac{T\Delta}{D} \right)^{1/4} \Delta T \quad (4)$$

For forced convection

$$C_w = 5.7 \times 10^{-3} \left(\frac{V}{D} \right)^{1/2} \Delta T \quad (5)$$

where D is the dimension of the leaf in the direction of the flow, which usually can be taken as the width of the leaf, V is the wind speed in the cm sec^{-1} , and ΔT is the difference between leaf and air temperature in $^\circ\text{C}$. The coefficients are such that C is expressed in $\text{cal cm}^{-2} \text{min}^{-1}$.

OBSERVATIONS

During the summer of 1963 an attempt was made to measure and evaluate the various terms in this equation for a site in the alpine tundra on Niwot Ridge, Colorado, above Science Lodge, at an altitude of about 11,000 feet. Solar radiation was measured with an Eppley pyrheliometer. A Gier and Dunkle hemispherical radiometer was used for the measurement of long wave infrared radiation from the atmosphere or from the ground. A Stoll-Hardy directional radiometer was used for observing the radiant temperatures of plant leaves, ground surface, and atmosphere. In the case of the ground radiation, R_g , and the atmospheric radiation, R_a , the measurements using the Stoll-Hardy radiometer were checked against the observations made with the Gier and Dunkle radiometer. These instruments are described by GATES (1962). In addition plant leaf temperatures were

observed using fine copper-constantan thermocouples with one junction inserted into the mesophyll of the leaf and the other junction either in the air, in the shade, or in an ice-water bath. Air temperatures at heights of 3, 10, and 100 cm were measured with fine thermocouples, and also wind speeds at these same heights. Wind speeds were measured with a hand held velocity meter of the torsion, fan type. Relative humidity of the air was measured with a sling-psychrometer.

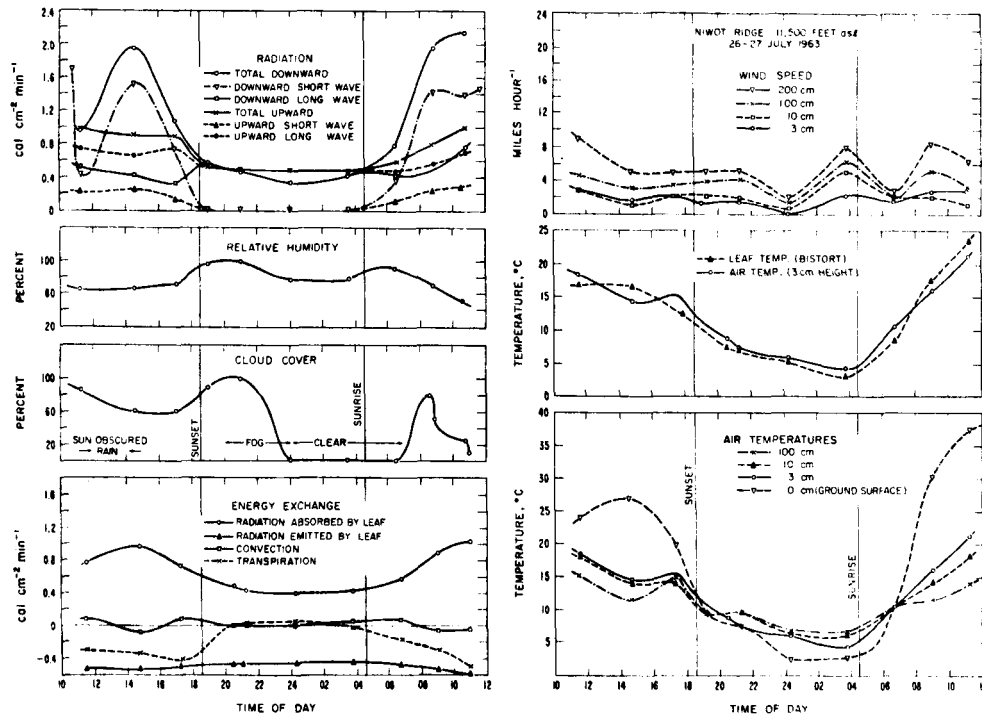


FIG. 8. — Microclimate measurements made on Niwot Ridge, Colorado at 11,500 ft., (3,504 m) above sea level on 26-27 July 1963. From the values of the microclimate parameters and the measurements of leaf temperature, the components of energy exchange were calculated for *Polygonum bistortoides* as shown.

The energy regime at the surface of the alpine tundra for a typical, partly cloudy, midsummer day, 26-27 July 1963, is shown in Fig. 8. The various radiations streams, short wave and long wave, upward and downward fluxes, are each shown separately. It is important to consider the individual streams, for a plant or animal will be coupled to the short wave solar radiation differently than to the long wave thermal radiation from the surroundings. From measurements by BIRKEBAK (1964), and GATES and TANTRAPORN (1952) on the absorptivity of plant leaves one can assume an absorptivity to sunlight, $a_1 = 0.52$, for deciduous leaves, and an absorptivity to infrared thermal radiation, $a_3 = \epsilon_t = 0.96$. Hence the plant

is coupled nearly twice as tightly to the infrared as to the solar radiation. This means that the temperature of the plant may often be more acutely determined by the thermal radiation from the surroundings, than from the sunlight, particularly when the amount of sunlight is only moderate. The amount of radiation absorbed by a leaf of *Polygonum bistortoides* is shown in the lower part of Fig. 8. The absorbed radiation must then be dissipated from the leaf by reradiation, convection, and transpiration, although convection may at times contribute energy rather than abstract energy.

The amount of sunlight received at the surface on 26 and 27 July, 1963, was not particularly strong since a great deal of overcast existed. The situation for clear days will be discussed later. From Fig. 8 it should be noted that there was always some wind for these days, even at the plant level. The wind speed fell rapidly as the ground surface was approached. When the wind speed was 8 mph at a height of 2 meters it was only 2 mph at a height of 3 cm. This sharp gradient in wind profile is without doubt a notable reason why alpine plants are not particularly tall. The effects of the physical environment observed here were measured and evaluated for a leaf of *Polygonum bistortoides*. The observed leaf temperatures are shown in Fig. 8. It is evident that during the period 26-27 July the leaf temperature remained very close to the air temperature at the level of the leaf. This is the result of two factors: the reduced solar heating of the leaf because of the cloud cover, and the constant presence of wind. It is interesting to note that for a considerable amount of the time the air was warmer than the leaf and therefore the convection term in the heat budget of the leaf was positive, although usually very small due to the slight temperature difference between the air and the leaf. A positive term in the energy budget implies energy transferred to the leaf. This is the result of two factors: the reduced solar heating of the leaf temperature being below air temperature, the transpiration rate must increase. This is clearly seen to occur about 1715 on 26 July. Transpiration will also be increased with an increase in the amount of radiation absorbed by the leaf as can readily be seen in Fig. 8.

The energy budget terms for the bistort leaf are all shown in the lower part of Fig. 8. The radiation emitted by the leaf was determined with the Stoll-Hardy radiometer and also by measuring the leaf temperature with thermocouples. The convection exchange was computed using Eqn. (4) or (5) and the temperature difference, ΔT , and wind speed V . For bistort the width of the leaf, D , was taken to be 2.0 cm. Finally the transpiration was computed from the other terms in order to balance Eqn. (3). The diurnal behavior of the calculated transpiration rate shown in Fig. 8 is entirely reasonable and the values are of the right order of magnitude.

In Fig. 9 is shown the same characteristics for a clear day, 2-3 September, during which the cloud cover was nearly always small. The wind speed was consi-

derably less during this period than during the period illustrated in Fig. 8. Although the midday air temperature was nearly the same for the two periods, the leaf temperature of *Polygonum bistortoides* was substantially higher on the clear, more calm, day. This increase in leaf temperature may be of considerable importance since certain biochemical processes, such as photosynthesis and respiration, may be strongly determined by leaf temperature. It should be noted that in terms of the energy budget computation, where transpiration is computed to balance the energy equation, that during a couple of hours of the night 26-27 July and all of the night 2-3 September, condensation of moisture on the leaf apparently was occurring. However, although the leaf was wet part of the time, it does not mean that condensation was always occurring. Since the transpiration term is computed as the difference in all the other terms in the energy budget, it could represent the accumulated error in the calculations.

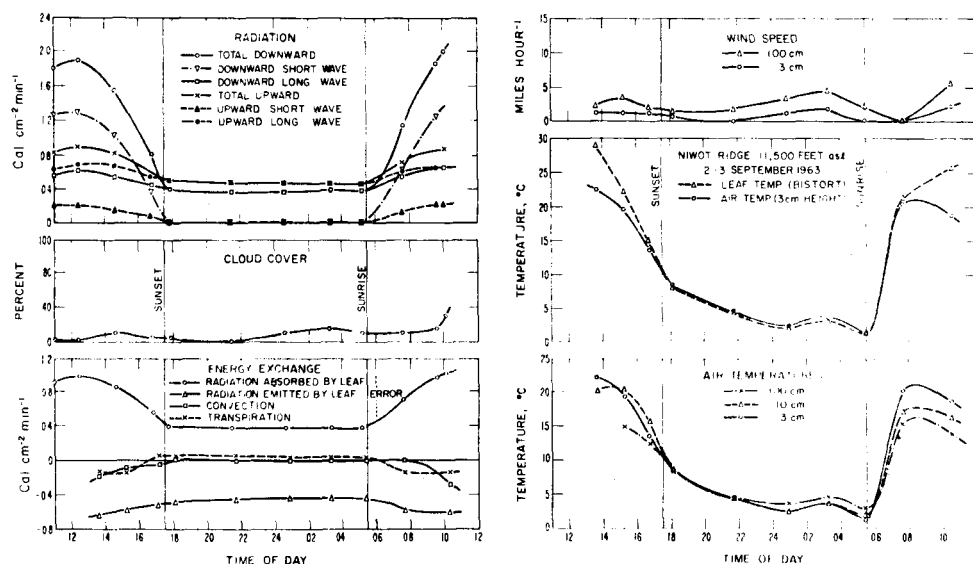


FIG. 9. — Microclimate measurements made on Niwot Ridge, Colorado at 11,500 ft. (3,504 m) above sea level on 2-3 Sept. 1963. From the values of the microclimate parameters and the measurements of leaf temperature, the components of energy exchange were calculated for *Polygonum bistortoides* as shown.

A few single observations of the temperatures of alpine plants which have been made on clear or partly cloudy midsummer days show that the plants may become very warm. On Niwot Ridge, at 10,000 feet, 22 July 1962, with clear sky and a few scattered cumuli and an air temperature of 18°C, sunlit leaf temperatures in still air were as follows: *mertensia* 27.3°C, *bistort* 28.2 to 29.1°C,

grass 29.1°C, moss campion 31.9 to 34.6°C; while soil containing seedlings of *Draba*, *Orioxous alpina*, *Sedum stenopetalum*, *Polygonum bistortoides*, *Artemisia scopulorum*, *Loida seratina*, and moss campion was at a temperature of 53.0°C and a bare aluvial soil had surface temperatures from 53.0 to 57.1°C. Some of the seedlings noted in this cluster had dead, dried leaves which were clearly « burned » and dessicated at these temperatures. Clearly the microclimate for these seedlings, which in their entirety were so close to the warm soil, was very severe and resulted in mortality to many seedlings and severe damage to others.

Leaf temperatures of alpine plants have also been reported by SALISBURY and SPOMER (1964) in which plant temperatures as high as 32.5°C were reported. They also report leaf temperatures as much as 20°C above air temperature.

The importance of measuring the air temperature at the level of the plant should be noted from Figs. 8 and 9 where the temperature at the 3 cm height may be considerably different than the temperature at 100 cm height; warmer near the surface during the daytime and cooler at night. In many instances the variation in air temperature from 3 to 10 cm above the surface is comparable with the variation from 10 to 100 cm.

The importance of the soil temperature and the air temperature near the surface was emphasized by BLISS (1956) when he stated « Of the environmental factors affecting growth rates of the various species at Umiat, it seems that soil and air temperature are most influential » and further « The controlling effect of higher temperature near the surface of the ground upon growth is clearly shown for *Alnus crispa* which leafed out 2 to 4 days earlier at the base of a clump than at the top of the same clump (1 m). The start of leaf expansion occurred 6 days earlier on the south side than on the north side of the same clump at Umiat. »

The radiation microclimate near the surface may have a diurnal cycle as shown in Fig. 10 in which the total radiation incident on two surfaces of the plant might be as high as $3.80 \text{ cal cm}^{-2} \text{ min}^{-1}$ or $1.90 \text{ cal cm}^{-2} \text{ min}^{-1}$. For these conditions the radiant energy absorbed by a leaf would be approximately $1.30 \text{ cal cm}^{-2} \text{ min}^{-1}$. The small leaves of these seedling may on occasion have temperatures above 55°C. In the absence of wind, with an absorbed energy of $1.30 \text{ cal cm}^{-2} \text{ min}^{-1}$, without transpiration, and with the energy dissipated only by reradiation and free convection the leaf temperature would reach approximately 58 °C if the air temperature near the surface was as high as 30 °C. A leaf temperature this high must be nearly lethal. It is, of course, possible that in the absence of wind and strong mixing that air temperatures in small protected pockets in the tundra would go even higher than 30°C for limited periods. At such times the mortality among small seedlings could be very high, since the radiation intensity is very strong. The small dimensions of alpine plants make the cooling by the air more effective than for plants of larger size. However, this will make only

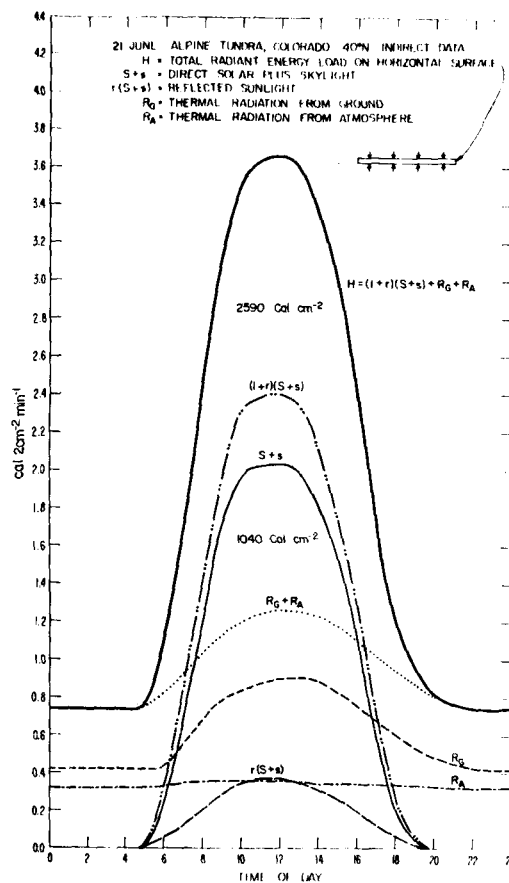


FIG. 10. — Diurnal variation of the radiation components incident on upper and lower surfaces of a horizontal leaf in the alpine tundra on a clear summer day. The downward direct and diffuse sunlight is $(S + s)$, sunlight reflected upward by the ground is $r(S + s)$, downward longwave thermal radiation from the ground surface is R_g , upward longwave thermal radiation from the ground surface is R_a , and the total radiation incident on the upper and lower surface is given in cal $2 \text{ cm}^{-2} \text{ min}^{-1}$.

a few degrees difference in temperature. The direct solar radiation incident on a horizontal surface at noon on a clear day with scattered cumulus clouds will often exceed the solar constant and reach a value as high as $2.20 \text{ cal cm}^{-2} \text{ min}^{-1}$. These strong amounts of radiation can be experienced by the mountaineer when he rests in the sun but is sheltered from the wind.

WIND AND CLIMATE

The wind velocity profile is also very dramatic in the tundra. Typical examples of the wind profile are shown in Fig. 11. It is very clear that the low, matted, alpine plants that grow in the tundra are living in the calmest strata to be found

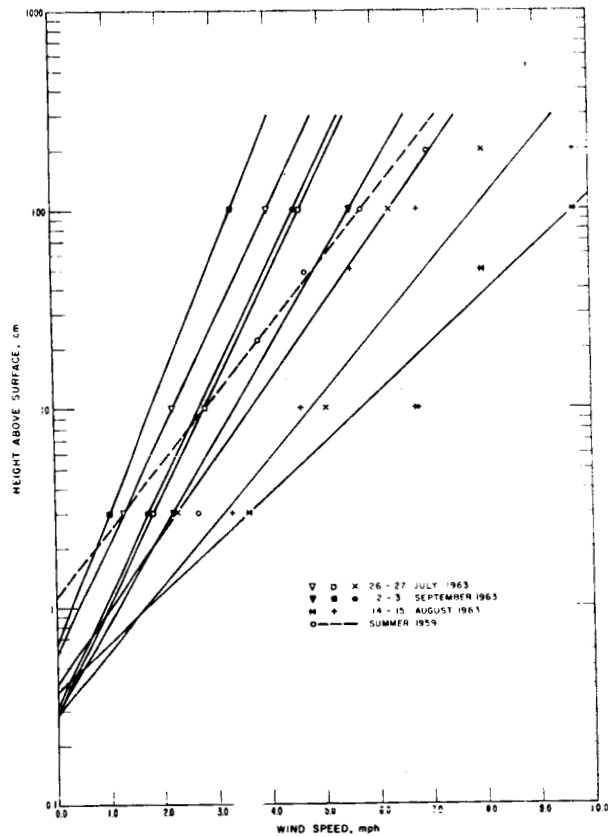


FIG. 11. - Measured wind speed as a function of height above the surface for the fell field on Niwot Ridge, Colorado at an elevation of 11,500 ft., (3,504 m) above sea level.

there. In fact the plant cover determines to a considerable extent the surface roughness and the resulting wind profile. Although the wind profile will change from position to position on the surface, the profiles shown in Fig. 11 are probably quite typical. A semi-log plot is used because it has been found that the wind

speed increases exponentially with the height above the surface, a relationship which can be expressed in the following form :

$$u = \frac{u_{200}}{k} \log \frac{z}{z_0} \quad (6)$$

where u_{200} is the wind speed at a height of 200 cm above the surface and z_0 a roughness parameter.

The roughness parameter is a description of the surface as it influences the flow of air over the surface. It depends on the vegetation cover, the rocks, and other terrain features. Once z_0 is known for the surface then the wind profile is always known. From Fig. 11 one can determine that z has a mean value of approximately 0.45 cm for the alpine tundra observed in late July, August, and early September. Individual values of z_0 varied between 0.26 and 0.65 cm. The nature of the tundra surface is quite variable and one can expect more of a variation in values than this, particularly as one goes from fairly sparse vegetation to a lush dense vegetation cover. Other investigators have obtained 0.1 cm for closely cropped lawn grass, 2.3 cm for thick grass 10 cm high, to 3.2 cm for an open field of high grass. The value of u_{200}/k in Eqn. (6) is approximately 1.8 mph.

Plant temperatures of plants of upright habit change inversely with wind speed. Since the wind speed is highly variable in the alpine tundra, plant temperatures may change quickly and frequently. Air temperature at the plant level during the daytime, when the surface is heated by sunlight, varies inversely with wind speed in that increased wind produces a mixing of the surface air with the air higher up and diminishes the air temperature. Equation (5) expresses the functional relationship of the cooling power of the wind on the vegetation.

An increase in wind speed will produce an increase in leaf cooling, and when accompanied by a sudden drop in the air temperature which accentuates ΔT , then the convective cooling becomes even stronger. This tends to bring the leaf temperature closer to air temperature when the leaf is fully sunlit. At night a reverse compensation occurs since the air will be warmer than the leaf and increased wind forces the convective transfer of energy to the leaf, hence warming the leaf, as well as mixing more warm air with the cooler surface air and accelerating the change in leaf temperature. The result of this activity is that ΔT tends to remain small and hence the leaf is close to air temperature.

The cushion plants will be more tightly coupled to the heat capacity of the ground than will the plants of upright habit. The temperature changes of these plants will lag behind the changes of the upright plants, but generally the maximum and minimum temperatures will be more extreme.

The influence of wind on the temperature of various parts of krumholtz having different exposures is very notable. The fully sunlit leaves on the lee side of an

Engleman spruce krumholtz averaged 29.7 °C, while those exposed leaves on top averaged 22.5 °C, with an air temperature of approximately 20 °C. The warmer leaves on the lee side will undergo a greater rate of photosynthesis, a greater productivity, and hence growth will be in the lee direction.

There is no question that the enormous predominance of wind in the alpine tundra, coupled with low air temperatures, is the primary reason for the limited growth and low habit of the plants. In parts of the world at low elevations, wind may be a decidedly beneficial factor as a mechanism for renewing the CO₂ concentration near the leaf surface and stimulating productivity, but in the alpine tundra wind is primarily detrimental. There may be occasions on clear or partly cloudy days when wind will be beneficial for the seedlings growing close to the soil. The soil temperature will become very warm in still air and wind will assist with cooling the surface.

ENERGY AND PHYSIOLOGICAL RESPONSE

The consequence of the environmental factors as they influence plants can be evaluated in terms of the physiological processes within the plants. One such process is photosynthesis. MOONEY and BILLINGS (1960, 1961) have measured in the field the carbohydrate cycle and photosynthetic rates for alpine plants.

SCOTT and BILLINGS (1964) have obtained in the laboratory measurements of the synthetic rate as a function of light intensity and temperature for several plant species normally found in alpine habitats. As a means of illustration the data obtained for *Geum rossii* will be used here as shown in Fig. 12. The striking feature concerning these curves of photosynthetic rate is the relatively low temperature for optimum activity, e.g. 8°C. This low optimum is present in the data for alpine races of the following species as well: *Arenaria obtusiloba*, *Artemisia scopulorum*, *Deschampsia caespitosa*, *Poa alpina*, *Potentilla diversifolia*, *Trifolium dasyphyllum*, *Trifolium parryi*. This is all the more interesting when one realizes that *Mimulus cardinalis* and *Mimulus lewisii* growing in the Sierra mountains of California has its optimum photosynthesis near 30 °C, see MILNER, NOBS and HIESEY (1964).

If one imagines a clear, still day for the alpine tundra which is relatively warm near the surface (maximum air temperature 29 °C) then the environmental conditions will vary diurnally as shown in Fig. 13. The temperature of sunlight exposed and unexposed plant leaves is given. If for the light intensity and leaf temperature combination which occurs throughout the day one determines the photosynthesis from Fig. 12, the values shown in the lower portion of Fig. 13 are obtained. The leaf temperatures were well above optimum during midday and for the exposed

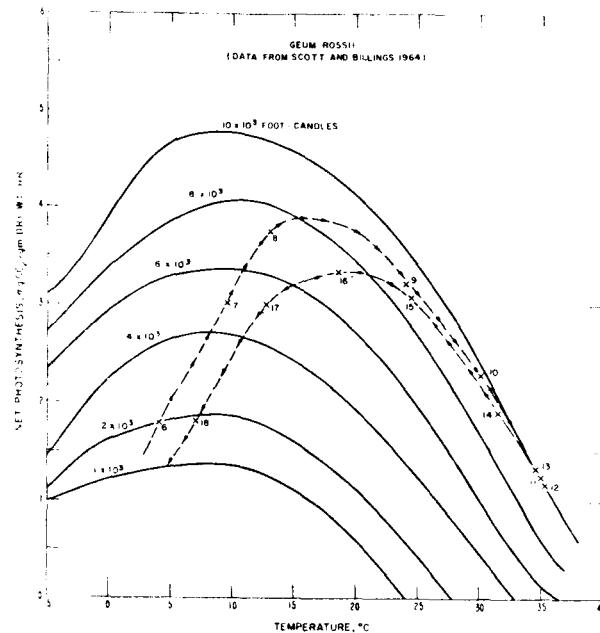


FIG. 12. — Net photosynthesis as a function of plant temperature and light intensity for *Geum rossii*. The diurnal net photosynthesis for a plant in the alpine tundra on a warm, still summer day is shown with the time given in hours.

leaves a strong decrease in photosynthesis would occur throughout this period. The shaded, unexposed leaf, though cooler, was not receiving as much sunlight and hence the total photosynthesis for it during the day amounted to 19.0 mg CO₂/gm dry weight compared with 31.2 for the fully sunlit leaf. At the light intensity given if an exposed leaf remained at an optimum temperature of 8 °C, then the photosynthetic curve shown would result with a total amount of 49.3 mg CO₂/gm dry weight. For comparison purposes a cloudy day situation is illustrated on the right hand side of Fig. 13. For the amount of light available on this overcast day the total photosynthesis of the exposed leaf (30.3), the unexposed leaf (31.8) and the optimum temperature condition (33.3) did not differ significantly.

It is clear from these comparisons that leaf temperature is a very important factor in the photosynthetic response to given light conditions. If most alpine plants truly have an optimum temperature for photosynthesis at 8 or 10 °C, then clearly a mechanism for reducing the leaf temperature during days of intense radiation is of vital importance. In this regard the ever present wind can contribute to the welfare of the alpine plants through its cooling influence on their temperatures. The wind also generates turbulence and mixing so that the cooler air above the surface is brought in contact with the warm soil. By producing cooler air at the

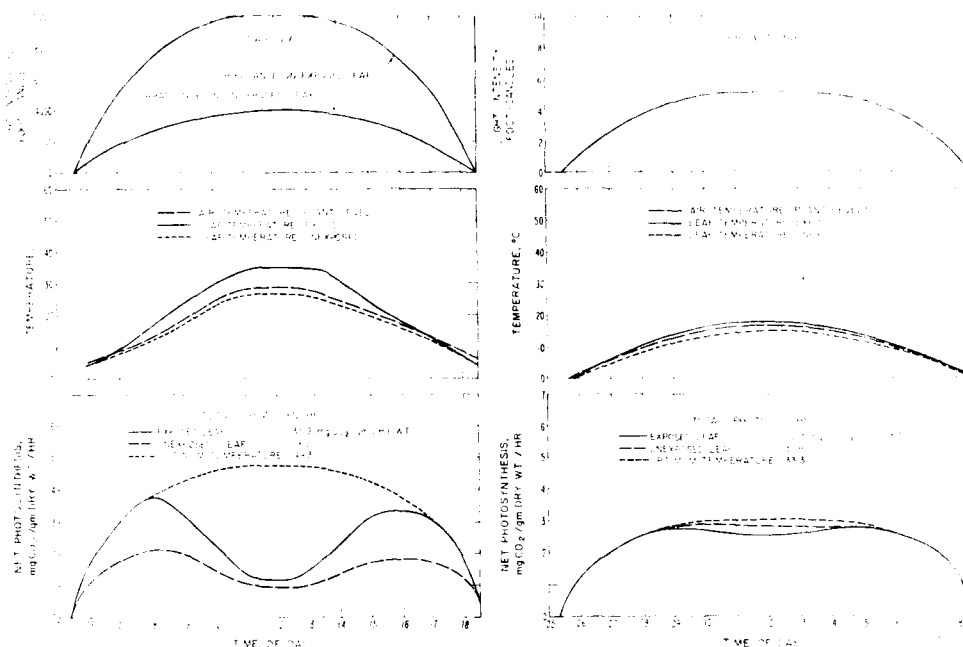


FIG. 13. — Hypothetical examples of the microclimate, leaf temperature, and net photosynthesis for an alpine plant on a warm, clear, still summer day and on a cool, cloudy, still summer day.

plant level and convective cooling of the plant, the wind is very effective in its influence on plant temperatures. On the other hand, during the spring, when air temperatures are low, the periods of relatively still air and warm soil temperatures may be most important in lifting plant temperatures to a suitable level for active photosynthesis to proceed.

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